

THE COURTSHIP CALL OF *CHRYSOPE DOWNESI* BANKS
(NEUROPTERA: CHRYSOPIDAE):
ITS EVOLUTIONARY SIGNIFICANCE*

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INTRODUCTION

Tauber and Tauber (1977a) suggest that the conifer-associated green lacewing *Chrysopa downesi* Banks evolved sympatrically in northeastern North America from its holarctic sibling *C. carnea* Stephens. The proposed mechanism of speciation follows the general theoretical model of Maynard Smith (1966) and specifically involves simple allelic changes at three loci, one controlling body color and two altering the insect's response to photoperiod (Tauber and Tauber, 1977b). Gene substitution at the first locus initially induced divergence in habitat association, while later substitutions at the other loci produced complete reproductive isolation of the two populations by causing each to breed at a slightly (but sufficiently) different time of year (Tauber and Tauber, 1976).

An alternative explanation of *C. downesi's* origin from *C. carnea* is proposed which invokes the concept of allopatric speciation (Mayr, 1963): two portions of a previously contiguous *C. carnea* population became physically isolated from one another for a period of time, perhaps by glaciation events; subsequently, removal or disappearance of the geographic or climatic barrier re-established contact between the two populations, but intervening, independent evolutionary changes prevented much or any gene flow (Hendrickson, 1978). Tauber and Tauber (1978) argue that allopatric or geographical speciation is a less parsimonious explanation of the existing data than the sympatric model, although they admit that their evidence does not truly discriminate between the two hypotheses. However, my studies of courtship and mating behavior in the two lacewing species indicate that, in this case, a traditional allopatric model may in fact be preferable to the more intriguing sympatric one.

*Manuscript received by the editor February 20, 1980

Implicit in most models of geographical speciation is the strengthening of reproductive isolation between imperfectly isolated populations after contact is re-established; in animals, behavioral patterns associated with courtship are thought to be particularly subject to alteration, since premating barriers are presumed to be less wasteful of reproductive effort, gametes, or offspring than those that intervene after copulation (Dobzhansky *et al.*, 1977). In lacewings of the genus *Chrysopa* Leach, I have shown that short-distance acoustical communication by substrate transmission of abdominal vibration or jerking is a necessary component of successful courtship (Henry, 1979, 1980). A different "calling" pattern characterizes each of the eight sympatric lacewing species that I have studied in detail, suggesting that abdominal jerking is or has been important to the reproductive isolation of lacewing species in eastern North America. This view is strengthened further by the fact that the most closely related species, particularly those of the subgenus *Chrysoperla* Steinmann,¹ predictably show the most distinctive and elaborate patterns. Since *C. carnea* and *C. downesi* are members of this latter taxon, the nature of their acoustical signals could indicate how they speciated. If their separation occurred within a single contiguous population by the simple genetic changes postulated by Tauber and Tauber, one would predict identity or at least similarity of calling pattern in both species, since (1) barriers to gene flow are presumed complete after the three allelic substitutions and (2) even casual attempts at interspecific matings are precluded by the Taubers' model. On the other hand, allopatric speciation followed by re-established sympatry should produce unmistakably different patterns of abdominal jerking in the two species, since different calls would terminate heterosexual interactions between them before copulation could occur. I propose that the latter alternative is consistent with the extreme calling differences that exist between the two siblings.

METHODS AND MATERIALS

Lacewing calls consist of discrete bursts or volleys of abdominal strokes (jerks); the call itself is actually a sequence of one or several different kinds of volleys repeated in characteristic temporal pat-

¹This taxon has been given full generic status by Y. Semeria (1977).

terns. The frequency with which the abdomen is jerked or vibrated during each volley is quite low and may be modulated (changed) during the brief course of the volley. A sexually receptive male and female of a given species will establish a duet of abdominal jerking during courtship; in such a duet, partners will alternately trade volleys, or whole sequences, without overlap or interference.

I recorded and photographed jerking activity using the equipment and techniques of a previous study (Henry, 1979). A ceramic transducer (crystal phonograph cartridge) picked up substrate vibrations produced in a thin plastic membrane by calling lacewings and fed these signals to a storage oscilloscope. Conclusions regarding the patterns of *C. carnea* were based on observations of many (more than 30) successful courtships performed by numerous pairs of individuals drawn from populations in Connecticut, New York, Illinois, and California; those concerning *C. downesi* were based on six successful and 15 unsuccessful courtships by eleven pairs (7 males and 10 females) from the northern Catskill mountains of New York State, observed for 69 hours. The source population of *C. downesi* was sympatric with that of *C. carnea* at the Catskill site. I did not find any geographical variation in *C. carnea*'s calling patterns.

RESULTS

Chrysopa carnea's call (Fig. 1) consists of a long sequence of 40 or more short (approximately 1/2 second) volleys of vibration; volleys are separated by 1-2 second intervals, and the sequences of two insects are interdigitated during duets—i.e., partners alternate volleys (Fig. 1A). The frequency of abdominal vibration is modulated during each volley, from around 100 strokes per second at inception to 35 or 40 per second at termination (Fig. 1B). Additionally, there is a gradual but significant change in the spacing of volleys during each solo or duet sequence (Henry, 1979). The calls of this species are not markedly sexually dimorphic.

In contrast, the call of the *C. downesi* male or female is more elaborate than and totally unlike that of *C. carnea* (Fig. 1C and Table 1). A sexually receptive individual will periodically release a 5-8 second (or longer) sequence of closely-spaced jerking volleys, punctuated by a sharp discontinuity where the duration of and interval between volleys abruptly change. Part one of each sequence consists of four to seven identical (except for gradually increasing

overall amplitude) volleys at $1/2$ second intervals; each volley itself lasts about $1/3$ second and is divided into a short, relatively intense initial section of 5-8 abdominal strokes and a longer, weaker portion of 20 or more strokes, every other one of which is usually emphasized (Fig. 1D). Part two consists of 10-20 distinctly different, shorter, simple volleys repeated every $1/5$ - $1/4$ second and each made up of 6-8 strokes of the abdomen; overall intensity is high at the onset of part two, but steadily declines almost to a null. Frequency of abdominal vibration is held fairly constant throughout, averaging 68-80 strokes/second. Duetting insects, rather than interdigitating their solo sequences in the manner of *C. carnea*, alternate entire sequences politely with one another. Again, sexual differences are not profound in *C. downesi*, although during duets female sequences are nearly always shorter than those of males (99 out of 127 sequences).

DISCUSSION

In summary, the calls of *C. carnea* and *C. downesi* differ greatly in overall complexity, duration, volley amplitude and frequency structure, and manner of exchange in heterosexual duets. Whereas *C. carnea* adults produce long homogeneous sequences of indeterminate length and rapidly exchange volleys of jerking when duetting, those of *C. downesi* produce more structured sequences composed of two distinct classes of volleys and patiently exchange entire sequences when duetting. Additionally, pronounced frequency modulation characterizes single volleys of *C. carnea* but not of *C. downesi*. If, as is likely, the divergent calls function primarily to prevent interbreeding², an allopatric origin of the two species is implicated. An alternative explanation of the observed dissimilarity in their "songs," genetic drift following sympatric speciation, is not as convincing. It requires that two species showing grossly different calling patterns also display striking morphological similarity (Tauber, 1974) and complete interfertility in the laboratory (Tauber and

²Species-specific calls can also originate in response to selective pressures unrelated to reproductive isolation—e.g., one type of call might communicate information more efficiently than another in a particular habitat. However, I am unable to identify any features of the two lacewings' normal habitats that are simultaneously important to the production of sound and sufficiently different to account for the divergent calling patterns.

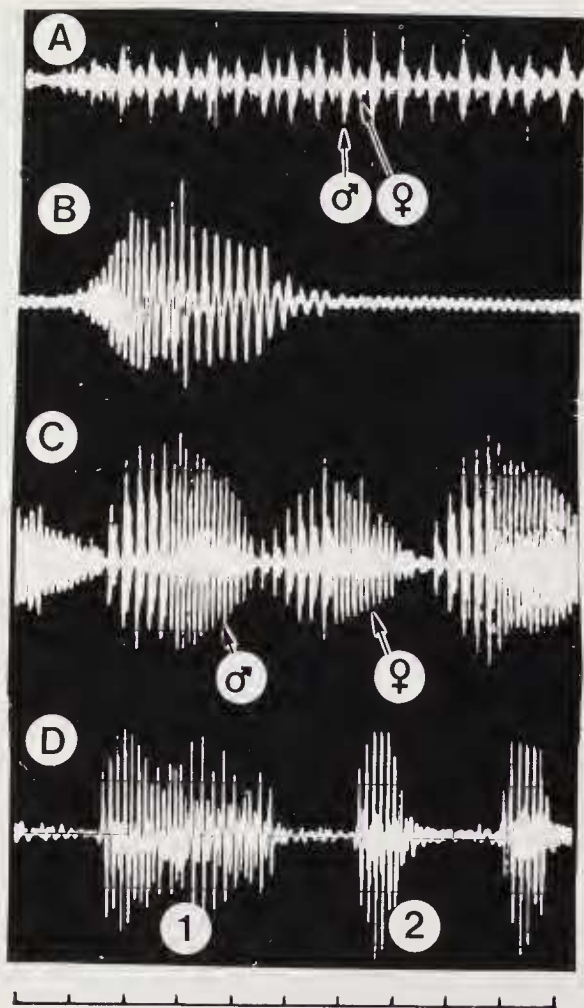


Figure 1. Oscillographs of abdominal vibration patterns produced by courting individuals of *Chrysopa carnea* (A, B) and *C. downesi* (C, D). Duets between a sexually receptive male and female are recorded in (A) and (C) at an oscilloscope writing speed of 2 seconds/major division; in *C. carnea*, each insect exchanges single volleys of abdominal jerking with its partner, while in *C. downesi*, whole sequences of volleys are exchanged. Individual volleys for each species are shown in B (*C. carnea*, male) and D (*C. downesi*, male), recorded at a writing speed of 0.10 second/major division. For *C. downesi*, volleys typical of part 1 and part 2 of the sequence are indicated.

| | | NUMBER OF VOLLEYS | INTERVAL BETWEEN VOLLEYS | NUMBER OF ABDOMINAL STROKES/VOLLEY | FREQUENCY OF ABDOMINAL VIBRATION | OVERALL DURATION OF CALL | INTERVAL BETWEEN CALLS |
|---------|--------|-------------------------|--------------------------------|--|---|--------------------------------|------------------------------|
| MALES | PART 1 | 5.29±1.32 (214, 7) | 0.56±0.05 (241, 7) | 25.69±4.46 (31, 3) | 78.29±5.49 (31, 3) | 6.76±1.48 (182, 7) | 13.47±2.21 (142, 7) |
| | PART 2 | 15.41±4.57 (190, 7) | 0.25±0.02 (246, 7) | 7.02±0.84 (45, 3) | 70.74±5.28 (47, 3) | | |
| FEMALES | PART 1 | 4.92±1.01 (169, 10) | 0.55±0.05 (196, 10) | 26.88±4.02 (36, 3) | 74.50±2.75 (35, 3) | 5.78±1.12 (153, 10) | 13.33±2.19 (138, 10) |
| | PART 2 | 13.04±4.30 (164, 9) | 0.25±0.02 (218, 9) | 6.84±0.85 (79, 4) | 69.32±4.86 (77, 4) | | |

Table 1. Important measurable characteristics of the calls (sequences) of males and females of *Chrysopa downesi*. Data from heterosexual, homosexual, and solo calls are pooled due to insignificant differences. Mean values and their standard deviations are tabulated; intervals and duration are in seconds, frequency in abdominal strokes per second. Sample sizes are entered parenthetically: the larger figure represents the number of calls measured, while the smaller one is the number of different individuals producing more than 10 of such calls. Parts 1 and 2 as in Fig. 1.

Tauber, 1977), whereas one expects random processes to affect all aspects of an organism's genotype more or less equally. This same interfertility and morphological similarity of the two species argue strongly for their close relationship to one another and against their having other closest relatives and other evolutionary histories.

ACKNOWLEDGEMENTS:

This study was supported by N.S.F. award number DEB77-12443, C. S. Henry, principal investigator. I thank the following colleagues from the University of Connecticut: R. Pupedis, J. O'Donnell and S. Cohen for help in the field collection and laboratory maintenance of lacewings; and R. J. Schultz, E. Brighty, and G. Clark for constructive comments on the paper and its concepts. C. Tauber, Cornell University, kindly supplied six of the *C. downesi* adults from a young laboratory colony.

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